NOTES

COMPARISON OF AMERICAN EEL GROWTH RATES FROM TAG RETURNS AND LENGTH-AGE ANALYSES

Estimates of growth rates of American eel, *Anguilla rostrata*, have been largely indirect, based on projections from length-age regressions or comparisons of mean lengths at particular ages (Smith and Saunders 1955; Boëtius and Boëtius 1967; Ogden 1970; Bieder 1971; Gray and Andrews 1971; Hurley 1972; Harrell and Loyacano 1980; Kolenosky and Hendry 1982). Although valid for many fish species, these two approaches may be questionable in eel studies because of high variability in lengths at given ages and because of considerable overlap in lengths among ages (e.g., Bertin 1956; Fahay 1978; Facey and LaBar 1981; Moriarty 1983). Testing the accuracy of a length-age regression as an estimator of growth rate requires a simultaneous mark-recapture study. Our objective was to mark and recapture eels in a Georgia estuary and to compare growth data from recaptures with growth estimates derived from length-age regressions and mean-length-at-age calculations for eels from the same population captured at the same time. We also sought information on seasonal growth patterns and differences in growth rates among size classes.

Materials and Methods

All American eels were captured in tidal Fridaycap Creek (lat. 31°21′N, long. 81°24′W) which enters the South Altamaha River, Ga., about 11 km from the river mouth (see Helfman et al. 1983). Salinities and water temperatures ranged from 0 to 22‰ and 5.5° to 31°C, respectively. Baited eel traps were set at or before sunset and pulled shortly after sunrise the next day. Animals were anesthetized in an ice slurry or in tricaine methanesulfonate, measured (total length), weighed, tagged with 25 mm long Floy[1] FD-68B anchor tags, and released where captured. We tagged 659 animals on eight occasions between October 1980 and December 1982. Growth data from eels at large <20 d were not used because of possible confusion with measurement error, which averaged ±1 mm (range = 0-5 mm, N = 35 measurements of seven eels).

Age determinations are based on sagittal otolith analyses from 305 eels captured concurrently with tagged animals. Most otoliths had distinct opaque and transparent zones, with few apparent supernumerary zones. Seasonal analysis of otolith margins indicated that presumed annuli were deposited on an annual basis and were a reasonable chronicle of age (Helfman et al. in press). Fish used in the mark-recapture study of growth were not collected for histological examination of gonads, and we therefore could not determine if sex-related differences in growth occurred (Tesch 1977).

Results

We recaptured 101 individuals, for an overall recapture rate of 15%. Time at large ranged from 8 to 493 d. Recapture frequencies were 84 fish recaptured once, 14 recaptured twice, 2 recaptured three times, and 1 recaptured four times.

Growth rates of recaptured eels were variable but fell into two apparent seasonal categories (Table 1): 1) Slow growth from November through February (0.0-0.08 mm/d, $\bar{x}$ = 0.026, SD = 0.024, N = 13 recaptures) and 2) fast growth during spring, summer, and fall (0.01-0.63 mm/d, $\bar{x}$ = 0.221, SD = 0.152, N = 78 recaptures); fast period growth was significantly greater (t-test, P < 0.001). Combining averages, and assuming a slow period of 4 mo, yield an average annual growth

TABLE 1.—Growth rates of recaptured American eels as a function of season and year. Values in the body of the table are numbers of animals with particular growth rates. Intervals for fastest and slowest rates are subdivided by 0.05 mm/d; other intervals are 0.10 mm/d.

	Slow growth period (Nov.-Feb.)[1]	Fast growth period (Mar.-Nov.)	
Growth (mm/d)	1980-81	1981	1982
0.00-0.05	12	2	4
0.06-0.10	1	5	12
0.11-0.20		10	9
0.21-0.30		7	9
0.31-0.40		3	4
0.41-0.50			7
0.51-0.60		1	4
0.61-0.65			1
$\bar{x}$ growth (mm/d)	0.026	0.182	0.246
SD	0.024	0.107	0.172

[1] An additional 26 eels at large from late November 1982 to early May 1983, i.e., encompassing primarily the slow growth period, grew an average of 0.054 mm/d (SD = 0.034 mm/d).

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rate of 57 mm for eels 270-500 mm long over the 2-yr studied (95% C.I. [confidence interval] = ± 8.4 mm, growth periods treated as independent random variables, Bliss 1967). Growth as percent increase in length for an average eel 347 mm long was 16%.

Accuracy of the extrapolated annual estimate can be tested against independent, long-term growth data from animals whose recapture intervals included both growth periods. Seven animals had recapture intervals of 6-16 mo (Table 2); average growth was 62 mm/yr (95% C.I. = ± 20.1 mm) or a 17% increase in length.

TABLE 2.—Annual growth rates of eels in Fridaycap Creek, Ga., based on long-term recaptures. Data are from eels that were at large for more than a 180-d interval that included both fast and slow growth periods.

	Date			Length (mm)			
Eel no.	First capture	Second capture	Days at large	Initial	Final	Growth rate (mm/yr)	Percent increase
[1]1	26-X-80	27-VIII-81	313	353	429	83	23
1	26-II-81	24-II-82	363	362	460	98	27
2	26-X-80	30-IV-81	186	328	351	45	14
3	7-III-81	24-II-82	353	378	450	74	20
4	26-X-80	27-VIII-81	306	487	511	24	5
5	19-II-81	24-II-82	369	307	352	45	15
6	7-III-81	24-II-82	354	433	504	73	17
7	7-III-81	13-VII-82	492	393	492	56	14
		$\bar{x}$		381		62	17
		SD		58		24	7

[1] Eel No. 1 was captured four times; growth between first and third and between second and fourth captures were analyzed separately.

When the data are grouped into 50 mm size classes, animals in the 350-400 mm class grew faster than smaller animals (Fig. 1); 95% confidence intervals for other size classes overlapped, although some overlap may result from small samples of larger animals. Similar trends in relative growth (percent increase in length) were apparent (Fig. 1): values overlapped in the smaller size classes, and the largest size class grew slower than the fast-growing 350-400 mm group.

Growth rates during fast growth periods (Table 1) suggest that animals grew faster in 1982 than in 1981 (t-test, one tail, df = 76, $P < 0.05$). Maximum growth rates also differed: the 5 fastest growth rates, as well as 13 of the 15 fastest rates, occurred in 1982 (Table 1).

Information on weight gain is less complete but shows a similar seasonal trend. Average weight increase between recaptures was 0.223 g/d (SD = 0.222, N = 47) for the fast growth period; limited data suggest lesser gains for the slow growth period (0.017-0.144 g/d, N = 2). When seasonal data are summed and a 4-mo slow growth period is assumed, annual weight increase was 63 g. Long-term weight change data from two animals at large 299 and 371 d indicate an average weight increase of 76 g/yr (range = 67 to 86 g/yr).

Mean lengths at different ages were

Age class (yr):	*II*	*III*	*IV*	*V*	*VI*	*VII*
$\bar{x}$ length (mm)	242	310	361	403	442	460
Range (mm)	197- 278	214- 446	233- 548	256- 570	297- 559	386- 500
N	6	51	134	78	32	5

The mean values project an average annual increase of 44 mm (range = 39-68 mm). The related length-age regression for all eels aged at this locale during the study period was length = 183.3 + 43.5 × age (N = 305, r = 0.492, $P < 0.01$) which also projects an average annual increase of 44 mm (95% C.I. = ± 8.7 mm) for an average eel 370 mm long.

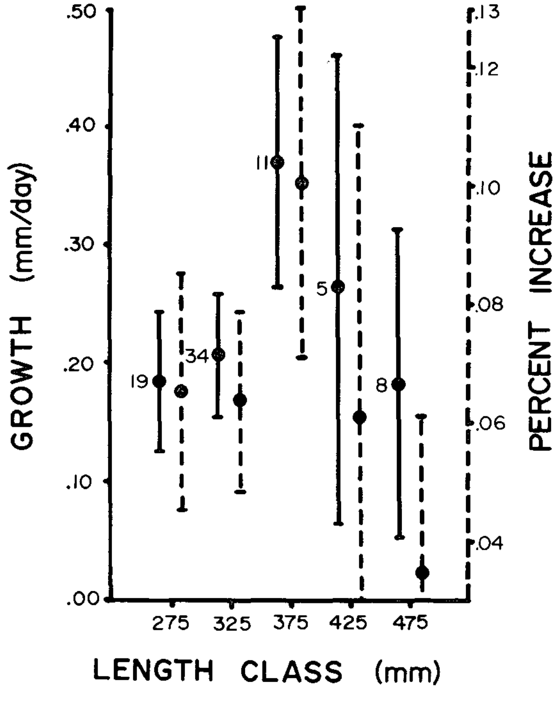

FIGURE 1.—Growth rates of recaptured American eels as a function of size at initial capture, Fridaycap Creek, Ga., October 1980-November 1982. Growth is expressed as the actual daily rate of increase (solid vertical lines, means ± 95% confidence intervals) and the percent increase as a function of initial length (dashed vertical lines, means ± 95% confidence intervals). Data are from fast growth periods, 1981 and 1982 combined. Numbers beside each mean are the total animals comprising each 50 mm size class. Midpoints of length classes are shown on x-axis.

Discussion

Comparisons of Growth Measures

Different procedures yielded different estimates of growth rate. The two independent, direct measures based on recaptures—seasonal summation and long-term recaptures—produced similar values (57 mm/yr and 62 mm/yr, respectively). The indirect measures—length-age regression and mean-length-at-age analysis—both projected annual growth rates of 44 mm/yr. All estimates are complicated by extreme variability in growth, with overlap in lengths among four to six year classes common (Smith and Saunders 1955; Ogden 1970; Gray and Andrews 1971; Hurley 1972). Growth rate estimates based on recapture data were apparently higher than those derived from length-at-age analyses, but confidence intervals overlapped among all estimates. However, we feel that the direct measures are more accurate. First, the sample size for the length-age analyses was more than three times larger than for the seasonal summation analysis, but the confidence intervals were very similar (17.4 mm and 17.8 mm, respectively), suggesting less variability in the recapture data. Second, growth rates derived from recaptured animals are based on actual growth between captures; variability in calculated growth rates should therefore reflect real variability in growth among animals. In length-age analyses, age classes are commonly resolved at no finer than an annual level. Consequently, growth subsequent to day 1 of each year increases the variance around the estimate rather than increasing the accuracy of the estimate. Finally, the accuracy of age determinations from otoliths in some eel populations is questionable (Moriarty and Steinmetz 1979; Deelder 1981; Casselman 1982), placing length-age analyses in doubt unless annulus formation can be verified.

Limited growth data from other mark-recapture studies of American eels are available. Hurley (1972) tagged 1,418 American eels in Lake Ontario, Canada, and reported recapture intervals for 13 large individuals (730-874 mm), which increased an average of 34 mm/yr. At two Louisiana freshwater locales, Gunning and Shoop (1962) tagged 43 American eels; only four recaptures provided usable data, indicating an average growth of 140 mm/yr (growth range = 46-325 mm, initial lengths = 255-915 mm). R. L. Haedrich[2] tagged 148 American eels in a Massachusetts estuary. Four individuals (initial lengths ≑ 500-700 mm) had an average annual growth rate of 6% (range = 4.1-8.4%). An inverse latitudinal trend in growth is suggested (see also Harrell and Loyacano 1980), but direct comparison is complicated by different initial lengths, small sample sizes, and high variability in growth.

Length-related differences in growth have also been found for other populations. A shift from allometric to symmetric growth occurred at 800 mm for American eels in Lake Ontario (Hurley and Christie 1982). Those authors, as well as Smith and Saunders (1955), related such a growth change to physiological preparation for maturation and migration. Gray and Andrews (1971) found that American eels in New Brunswick, Canada, estuaries grew slowly after age XI. Helfman et al. (in press) suggested that maturation of Fridaycap Creek eels occurred at around age IV (mean length = 387 mm). An apparent decrease in growth rates of Fridaycap Creek animals longer than 400 mm (Fig. 1) supports their interpretation.

Causes of Seasonal Differences

Seasonal and annual differences in growth rate can be linked to fishing success as affected by climate. Eel fishing in Georgia estuaries is typically poor at water temperatures below 10° C and above 24° C. In 1980-81, estuarine water temperature fell below 10° C during December 1980, but average 1981-82 monthly temperatures were higher and did not reach the 10° minimum until January 1982. In addition, rainfall in 1981 was 45 cm below average, and mean water temperatures were 2° C higher during June through September than in 1982 (R. Arnsdorff[3] and T. E. Targett[4]). The winter slow growth period may therefore result from colder water temperatures and reduced feeding. Faster growth in 1981 than in 1982 may have resulted from elevated temperatures during much of the fast growth period of 1981. High water temperatures—leading to reduced feeding, interrupted growth, and poor fishing—occurs in European eels, *Anguilla anguilla* (Deelder 1981). Interrupted summer growth may

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[2] R. L. Haedrich, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X9, pers. commun. April 1983.

[3] R. Arnsdorff, Georgia Department of Natural Resources, Environmental Protection Division, 270 Washington St. S.W., Atlanta, GA 30334, pers. commun. October 1982.

[4] T. E. Targett, Skidaway Institute of Oceanography, P.O. Box 13687, Savannah, GA 31406, pers. commun. October 1982.

have occurred in our study population, but because we lack growth data from midsummer only, we cannot test for it.

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